

which proves the statement, since the principle directions of  $Ti^k$  are indeterminate.

Thus a necessary and sufficient condition that an electron describe a geodesic is that the principle directions of  $\Delta ik$  are indeterminate.

<sup>1</sup> Eddington, *Mathematical Theory of Relativity*, p. 120.

<sup>2</sup> Eddington, *Ibid.*, p. 182.

<sup>3</sup> Ricci, *Atti R. Ist. Veneto*, 62, 1230.

<sup>4</sup> *Proc. Nat. Acad. Sci. Washington*, 9, 175 (1923).

<sup>5</sup> Eisenhart and Veblen, *Ibid.*, 8, p. 19.

<sup>6</sup> Weyl, *Space, Time and Gravitation*, Section 28.

<sup>7</sup> Einstein, *Sitz. Pr. Ak. Wiss.*, April, 1919.

<sup>8</sup> Eisenhart, *Proc. Nat. Acad. Sci.*, 8, p. 28.

## LINKAGE OF DUTCH, ENGLISH, AND ANGORA IN RABBITS

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In 1919<sup>1</sup> I presented evidence that in rabbits two patterns of white spotting, English and Dutch, are either allelomorphs or closely linked with each other. English pattern is dominant over self in crosses; Dutch may be called recessive, although Dutch cross-breds usually show the Dutch character feebly expressed. A cross between English and Dutch produces English marked rabbits, similar in appearance to homozygous English, although they are really English-Dutch heterozygotes. Such  $F_1$  heterozygotes form two (and only two) kinds of gametes, so far as experiments have been carried. They transmit *either* English or Dutch, but no gametes are formed which transmit *neither* of these patterns as would be expected if the two are not allelomorphs. This conclusion was based on a study of 192 cases. Possibly a study of a larger number of cases would show the occurrence of cross-overs. For in rats we obtained no cross-overs between red-eyed yellow and albinism until some 400 or 500 cases had been studied. Then linkage was observed so nearly complete that only a fraction of one per cent of crossing-over has ever been found.

Subsequently it was found that English pattern is linked with angora coat. The cross-over percentage, as estimated from 1233 young produced by a back-cross between  $F_1$  animals and double recessives, is  $13.70 \pm 0.96$ . For female  $F_1$  parents alone, the case with which comparison will presently be made, the cross-over percentage is  $11.94 \pm 1.97$ .

If English and Dutch are linked with each other, and English is linked

with angora, Dutch also should be linked with angora; and if the linkage of English with Dutch is close, each should show about the same amount of linkage with angora as the other does. This has been found to be true.

In January 1921 a cross was made between self angora rabbits and Dutch short-haired rabbits. The  $F_1$  animals were all short-haired and showed a low grade of Dutch, usually within grades 1-3<sup>1</sup>. The  $F_2$  generation contained approximately the expected 25 per cent of angoras, and 25 per cent of high-grade Dutch (grades 12-16) but all of the latter were short-haired. This result indicated the existence of linkage, but gave no indication of its exact strength. To ascertain this the back-cross of  $F_1$  with the double recessive was needed. But first the double recessive had to be produced, since none had appeared in  $F_2$ . By testing individual  $F_2$  extracted homozygous (high-grade) Dutch against angoras, a few Dutch were found which were heterozygous for angora. In the production of such individuals, a cross-over gamete bearing both Dutch and angora had united with a non-cross-over gamete bearing Dutch and short hair.

Mating together these Dutch individuals heterozygous for angora, the desired double recessive combination was secured, homozygous both for Dutch and for angora. Two males of this constitution born in the spring of 1923 have now been back-crossed with  $F_1$  females, giving a direct measure of the linkage by the departure observed from a 1:1:1:1 ratio. To date 68 young from these matings have been reared to an age when they can be classified as to hair-length. The Dutch pattern is of course recognizable at birth. These young include 37 high-grade (homozygous) Dutch, of which 36 are short-haired and one an angora. There are also 31 low-grade (heterozygous) Dutch, of which 25 are angora and 6 short-haired. The indicated cross-overs are thus 7 in 68 or  $10.3 \pm 4.09$  per cent.

In testing linkage between English and angora, this same type of mating ( $F_1$  female x double recessive male) has given 293 young with an indicated cross-over percentage of  $11.94 \pm 1.97$ , which, considering the size of the probable errors, is rather close to the result in the case of Dutch and angora.

Until larger numbers have been studied it will be impossible to say whether English and Dutch are allelomorphs or closely linked, but that they are both in a common linkage system with angora is fully established.

Races of Dutch rabbits vary greatly in the grade of development of the Dutch pattern. This I have explained<sup>1</sup> on the basis of multiple allelomorphism, but Punnett<sup>2</sup> and Pap<sup>3</sup> have interpreted it as due to multiple independent factors. A study of the linkage relations of different types of Dutch rabbits will afford a basis for deciding which of these conflicting views is correct.

<sup>1</sup> *Publ. Carnegie Inst. Wash.*, No. 288, 1919.

<sup>2</sup> Punnett, R. C., *J. Genet.*, 9, March, 1920.

<sup>3</sup> Pap, E., *Zeit. ind. Abst. Vererb.*, 26, 1921.